Transactions of the American Fisheries Society 133:922–931, 2004
© Copyright by the American Fisheries Society 2004

Responses of Native and Nonnative Fishes to Natural Flow Regime Mimicry in the San Juan River

DAVID L. PROPST*

Conservation Services Division, New Mexico Department of Game and Fish, Post Office Box 25112, Santa Fe, New Mexico 87504, USA

KEITH B. GIDO

Division of Biology, 232 Ackert Hall, Kansas State University, Manhattan, Kansas 66506, USA

Abstract.—The maintenance or restoration of natural flow regimes has been proposed as one means of conserving native fishes. Native fish conservation is enhanced either through the restoration of natural fluvial geomorphic processes (and thus the maintenance of essential habitats) or by the suppression of nonnative fishes. The San Juan River of Colorado, New Mexico, and Utah was dammed in 1962 and its natural flow regime was lost. Beginning in 1993, the river was regulated to mimic a natural flow regime by increasing reservoir releases to mimic timing, but only partially to mimic amplitude, volume, and duration of spring snowmelt discharge. We evaluated the responses of native and nonnative fishes to this natural flow regime mimicry by comparing their autumn densities (number/m^2) in San Juan River secondary channels to those during spring runoff and summer base flow over a 9-year period. Densities of native speckled dace *Rhinichthys osculus*, bluehead sucker *Catostomus discobolus*, and flannelmouth sucker *C. latipinnis* increased with elevated spring discharge. Total native fish density was 10 times greater in 1993 (the year of highest spring discharge) than in 2000 (the year of lowest spring discharge). Collectively, nonnative fish density was negatively related to spring discharge, but western mosquitofish *Gambusia affinis* was the only commonly collected nonnative that had a significant relationship. Mean daily summer discharge did not affect the density of native or nonnative fishes. Nonnative fishes, however, responded positively to sustained low summer flows (days discharge was less than 14 m^3/s). Densities of red shiner *Cyprinella lutrensis*, common carp *Cyprinus carpio*, and western mosquitofish were four or more times greater in 2000 (a year of sustained low summer discharge) than in years with comparatively high summer discharge. Speckled dace was the only native species negatively affected by extended low summer discharge. Our results suggest that manipulating spring discharge to mimic a natural flow regime enhances native fish recruitment but might have limited effect in suppressing nonnative fishes, particularly fecund, rapidly growing, small-bodied species.

The maintenance or restoration of natural flow regimes has been proposed to conserve native fish assemblages (e.g., Tyus 1992; Stanford et al. 1996; Poff et al. 1997). Support for the natural flow paradigm derives, in part, from opportunistic studies wherein data on pre- and postflood fish assemblages were compared. Minckley and Meffe (1987) showed that native fishes were less vulnerable to floods than nonnatives in southwestern streams. In unregulated streams, pre- and postflood differences were often substantial (particularly in canyon-bound streams) and, in some cases, nonnative fishes were temporarily eliminated. They reported that in regulated streams, routine releases generally had no measurable effect on either native or nonnative fishes, but large volume reservoir releases occasionally removed nonnative fishes. Baltz and Moyle (1993) suggested that in unregulated streams in California the abundance of summer- or autumn-spawning nonnatives was limited by variable spring flows and predation of larvae and young by native Sacramento pikeminnow *Ptychocheilus grandis* and rainbow trout *Oncorhynchus mykiss*. More recently, Marchetti and Moyle (2001) provided empirical support for the positive effects of natural flow regimes on native fishes and the concomitant negative impacts on nonnative fishes. They found that natural flow regimes shifted environmental conditions (particularly water temperature and habitat) to the benefit of native fishes and high flows flushed some nonnative fishes from Putah Creek.

All major rivers in the American Southwest are regulated to some extent by dams, and, in most cases, nonnative species diversity and abundance are greatest in the regulated reaches of these rivers

* Corresponding author: dpropst@state.nm.us

Received March 9, 2003; accepted December 22, 2003

(Fuller et al. 1999). Although it is unlikely that major dams on these rivers will be removed, at least for the conservation of native fishes, it might be possible to manipulate flows to benefit native fishes while curtailing nonnative fish abundance.

The San Juan River, a major tributary of the Colorado River, historically supported at least eight fish species (Tyus et al. 1982). Currently, only speckled dace *Rhinichthys osculus*, bluehead sucker *Catostomus discobolus*, and flannelmouth sucker *C. latipinnis* are comparatively widespread and common in the river. Roundtail chub *Gila robusta*, Colorado pikeminnow *Ptychocheilus lucius*, and razorback sucker *Xyrauchen texanus* are rare, and Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* and mottled sculpin *Cottus bairdi* do not occur in the study area. Over 20 nonnative fish species have been collected (D. L. Propst and K. B. Gido, unpublished data). Of these, red shiner *Cyprinella lutrensis*, common carp *Cypinus carpio*, fathead minnow *Pimphales promelas*, channel catfish *Ictalurus punctatus*, and western mosquitofish *Gambusia affinis* are common in warmwater stream reaches. Four of these (red shiner, common carp, channel catfish, and western mosquitofish) are regularly identified as having negative impacts on native fishes (e.g., Meffe 1985; Ruppert et al. 1993; Tyus and Saunders 2000).

Previously, we reported (Gido et al. 1997; Gido and Propst 1999) on small-scale temporal and spatial variations in San Juan River fish assemblage structure and habitat use. Those studies provided insights into patterns of habitat use and assemblage structure in response to varying environmental conditions within a 2-year period, but did not elucidate responses of common San Juan River fishes to long-term flow manipulation to benefit native fishes. In this study, we used data from 1993 through 2001 to characterize the effects of a quasinatural flow regime upon native and nonnative fishes in San Juan River secondary channels. Under this flow regime, we expected that high spring discharge would have a positive effect on the autumn density of native fishes and a negative effect on nonnative fish density. We did not expect summer discharge to affect native fish density but anticipated that elevated summer discharge would negatively affect summer-spawning nonnative fishes. Specifically, our objectives were to (1) characterize the relationship between flow regime and the density of common native and nonnative fishes in the San Juan River, (2) contrast responses of native and nonnative fishes to a quasi-natural flow regime, and (3) use this information to evaluate whether a mimicked natural flow regime would benefit native fishes in the San Juan River.

Study Area

The San Juan River arises in the San Juan Mountains of southwestern Colorado and flows about 484 km to Lake Powell on the Colorado River (Figure 1). The San Juan River has few permanent tributaries and all, except the Animas River, normally contribute little to its total discharge. During much of the year, discharge is largely controlled by releases from Navajo Reservoir (operated primarily as a water storage and irrigation delivery reservoir). During summer, however, storm-induced inflows, including those of intermittent tributaries, can substantially increase the discharge of the river.

In 1991, the U.S. Fish and Wildlife Service issued a Biological Opinion, under authority of the Endangered Species Act, to the U.S. Bureau of Reclamation regarding the construction of the proposed Animas–LaPlata Project. Among the conditions of that Biological Opinion was operation of Navajo Dam to mimic a natural flow regime for the benefit of federally protected Colorado pikeminnow and razorback sucker. Beginning in 1993, releases from Navajo Reservoir were elevated during spring to simulate snowmelt runoff, but discharge after spring runoff recession remained similar to postdam flows.

Prior to its impoundment by Navajo Dam in the early 1960s, the San Juan River had a natural flow regime characteristic of southwestern rivers, with considerable intra- and interannual variation (Table 1). Mean daily discharge during spring ($\geq$283 m^3/s [10,000 ft^3/s {cfs}]) for five or more days occurred in almost half the years of record. Mean daily discharge ($\leq$14 m^3/s [500 cfs]) during summer was common. Following impoundment, mean daily discharge during spring snowmelt was diminished considerably (61% of predam). Average summer mean daily discharge was nearly the same, but annual variation was considerably reduced. During our study, mean daily spring discharge was less than preimpoundment discharge (73%), but was greater than postdam spring discharge (123%). Average summer mean daily discharge was similar among predam, postdam, and study periods, but periods of low summer discharge ($\leq$14 m^3/s) were considerably more common in the predam than in the postdam or study period.

In our study reach between Shiprock, New Mexico, and Chinle Creek, Utah, discharge was frequently divided among the primary channel and

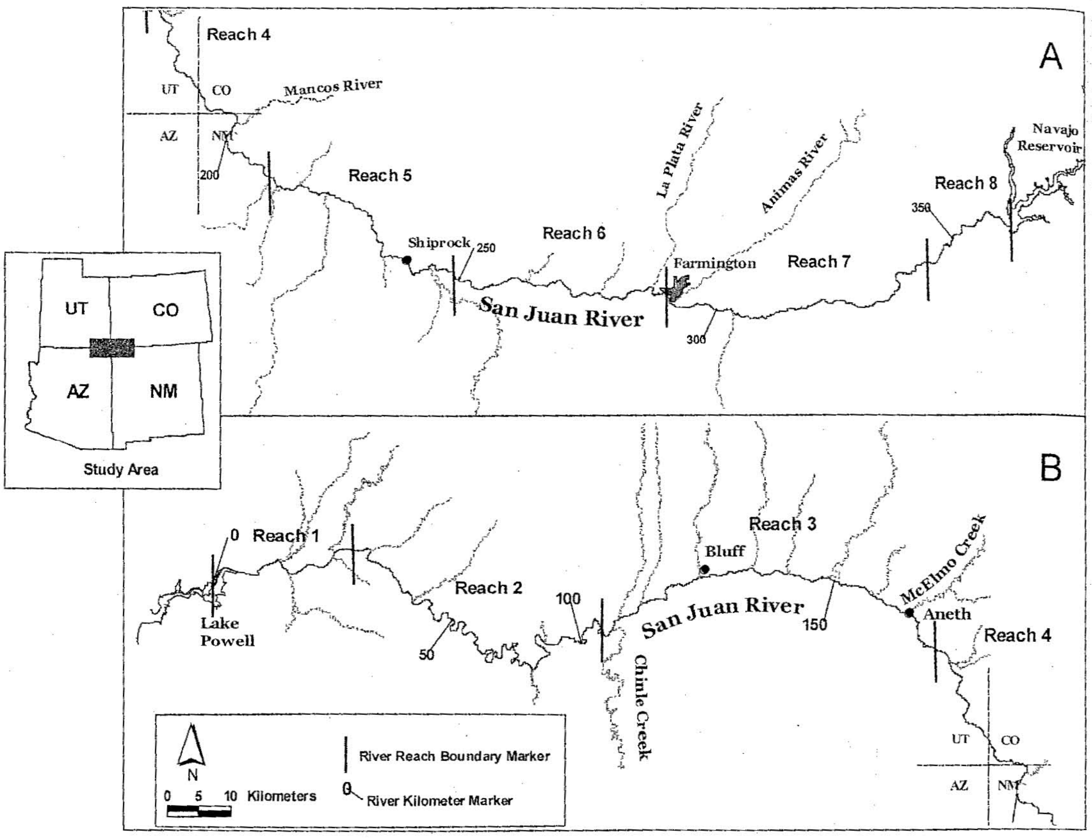

FIGURE 1.—Map of the San Juan River, Colorado, New Mexico, and Utah. Vertical bars denote reach boundaries defined in text (see Study Area), and numerals with a line indicate river kilometers (river kilometer 0 is at the historical confluence of the San Juan and Colorado rivers). Research for this study was conducted in reaches 3, 4, and 5.

one or more secondary channels. Collections from secondary channels were the focus of this study because they provided abundant habitat for small native and nonnative fishes and were readily sampled with seines. Secondary channels were defined as those with 25% or less discharge (visually estimated) at the time of sampling and measuring 200 m or longer. Secondary channels with inflow

TABLE 1.—Comparison of preimpoundment (1935–1961), postimpoundment (1962–1991), and study period (1993–2001) discharge attributes of the San Juan River. Data are summarized from U.S. Geological Survey's Shiprock, New Mexico, gauge (number 09368000); Q = mean daily discharge (m^3/s); values in parentheses = coefficient of variation of spring and summer mean daily discharge (derived from monthly mean daily discharge) or percent occurrence of the discharge attribute.

Attribute	Preimpoundment	Postimpoundment	Study period
Spring Q	135.9 (80.9)	82.5 (78.3)	98.1 (69.0)
Range of spring Q	42.7–310.2	13.3–202.9	41.7–171.9
Summer Q	44.8 (104.4)	46.2 (86.3)	45.7 (85.1)
Range of summer Q	9.1–151.6	13.4–121.4	14.9–124.1
Years spring $Q \geq 283$ m^3 (≥ 5 d)	11 (42)	5 (17)	2 (22)
Years spring $Q \geq 227$ m^3 (≥ 5 d)	14 (54)	8 (27)	4 (44)
Years spring $Q \geq 142$ m^3 (≥ 5 d)	23 (88)	13 (43)	7 (78)
Years summer $Q \leq 14$ m^3 (≥ 5 d)	21 (81)	17 (57)	6 (67)
Years summer $Q \leq 7$ m^3 (≥ 5 d)	12 (46)	9 (30)	1 (11)

typically had surface water their entire course and a variety of habitats (e.g., riffles, runs, shoals, pools, and backwaters). The habitat of those without inflow was mainly pool. The width of most secondary channels was 3–5 m, and a few were 10 m or wider their entire course. Maximum depths ranged from 10 cm or less in shallow runs to 2.0 m in pools. Substrata were cobble and gravel in riffles, gravel and sand in runs, and sand and silt in pools and backwaters. Instream obstructions (such as boulders, uprooted trees, and debris piles) contributed to pool formation.

Because physical differences within the San Juan River might affect the response of fishes to different flow regimes, the river was divided into six distinct geomorphic reaches (Bliesner and Lamarra 2000). Our study area encompassed three of these reaches: reach 3 (river kilometer [RK] 110 to RK 173; RK 0 is at Piute Farms, the historical confluence of the San Juan and Colorado rivers), reach 4 (RK 173 to RK 211), and reach 5 (RK 211 to RK 248). Cobble and gravel were the predominant substrata in most reach 5 secondary channels. Reach 4 was geomorphically transitional between reaches 5 and 3; sand was common, but cobble and gravel were present in most reach 4 secondary channels. Sand and silt were the most common substrata in reach 3, and sand was mixed with cobble and gravel where these were present. Riparian vegetation (mainly Russian olive *Elaeagnus angustifolia* and tamarisk *Tamarix chinensis*) was denser along reach 5 secondary channels than reaches 4 and 3. Reach 3 channels tended to be broader and less shaded than those in upper reaches.

Methods

Fishes were collected during daylight from an average of 33 (range, 18–45) secondary channels per year between late September and mid-October of 1993 through 2001. Each habitat (e.g., pool, undercut bank, shoal, run, and riffle) present in a secondary channel was sampled in rough proportion to its availability. Fishes were collected from each habitat with drag seines (4.6 m × 1.8 m, 3.2-mm mesh). All large-bodied (>100 mm total length [TL]) native fishes captured were identified, enumerated, and released alive. All specimens of Colorado pikeminnow collected were probably individuals stocked between 1997 and 1999; therefore, it was not considered in our analyses. Fishes in each seine haul were inspected to determine the presence of roundtail chub, Colorado pikeminnow, or razorback sucker; any found were released. All remaining specimens were preserved in 10% formalin and returned to the laboratory for identification and enumeration. The area of each seine haul was determined after fish sampling was completed.

Data from annual fish collections were grouped by geomorphic reach. Each reach was treated as a statistically independent entity rather than as longitudinal replicates because of marked differences in physical habitat among reaches. Fish density was the number of specimens of a species collected per total area sampled in the same reach. To reduce effects of disproportionately large values in analyses, fish densities were $\log_{10}(x + 1)$ transformed.

Four attributes of spring (1 March through 30 June) and seven of summer (1 July through 30 September) discharge (Table 2) were considered for evaluating associations with autumn fish density. Discharge data used in analyses were obtained from the USGS Shiprock gauge (number 09368000). We defined summer flow spikes as periods when mean daily discharge doubled within a 1–3-d period. The duration of flow spike was defined as days from initiation of increase through return to a level that remained relatively constant for at least 7 d. Postspike flow sometimes remained considerably higher than prespike flow.

To reduce the number of flow attributes used in our analyses, we examined covariance among variables using Pearson product-moment correlations and eliminated variables that were redundant (i.e., significantly correlated, $P < 0.05$). All spring and all summer discharge attributes (except days when discharge was less than 14 m^3/s) were significantly correlated. We therefore used mean daily spring discharge, mean daily summer discharge, and days of mean daily summer discharge of less than 14 m^3/s as the summary indices of annual discharge. We then used MANOVA (SAS Version 8.1, PROC GLM) to evaluate the effects of discharge upon the autumn density of native and nonnative fishes. Because native (three species) and nonnative (six species) fishes may differ in their response to discharge, we ran separate tests with species from these groups as dependent variables. In addition, we tested the effects of spring discharge, summer discharge, and days summer discharge less than 14 m^3/s separately for each group (with reach included as a categorical independent variable in all models). If an overall model was significant ($P < 0.10$), we ran individual models to evaluate interspecific differences in response to discharge. Correlation analyses were used to determine if the species response was positive (i.e., autumn density

TABLE 2.—Attributes of spring and summer discharge (m^3/s) in the San Juan River, 1993–2001. See the caption to Table 1 for additional information.

Attribute	1993	1994	1995	1996	1997	1998	1999	2000	2001
Spring									
Discharge									
Mar	144.4	25.1	78.7	19.8	58.3	32.3	24.6	26.7	29.3
Apr	169.1	24.6	98.4	15.1	65.0	40.4	30.8	46.8	39.2
May	180.9	135.1	173.0	56.6	161.6	148.7	89.9	65.5	135.4
Jun	193.1	185.9	264.9	75.4	234.7	112.5	161.9	57.0	134.8
Mean	171.9	92.7	153.8	41.7	129.9	83.5	76.8	49.0	84.7
Days $Q > 85$ m^3/s	122	55	97	16	67	48	41	18	47
Days $Q > 142$ m^3/s	105	43	55	0	44	24	26	1	29
Days $Q > 227$ m^3/s	11	7	21	0	26	0	0	0	1
Summer									
Discharge									
Jul	26.1	28.9	93.0	15.9	61.3	47.2	88.3	9.2	19.5
Aug	38.1	15.1	44.2	13.9	65.3	27.2	162.2	17.1	32.1
Sep	40.6	30.5	33.8	25.2	66.9	18.2	117.8	18.4	15.6
Mean	34.9	24.8	57.0	18.3	64.5	30.9	122.8	14.9	22.4
Days $Q > 85$ m^3/s	4	0	0	0	18	1	71	0	0
Days $Q > 57$ m^3/s	10	2	13	0	30	11	89	0	5
Days $Q < 28$ m^3/s	37	54	13	55	7	55	0	91	74
Days $Q < 14$ m^3/s	0	20	0	39	0	15	0	45	23
Flow spike duration (d)	35	15	29	22	66	37	92	7	18
Spike Q mean (m^3/s)	53.2	40.7	45.0	35.5	70.2	51.0	122.7	24.1	45.2

increased with high spring or summer discharge) or negative (i.e., autumn density decreased).

Results

Between 1993 and 2001, 6 native and 11 nonnative species were collected in San Juan River secondary channels between Shiprock, New Mexico, and Chinle Creek, Utah. Three native (speckled dace, bluehead sucker, and flannelmouth sucker) and four nonnative (red shiner, fathead minnow, channel catfish, and western mosquitofish) fishes were collected in all years. Plains killifish *Fundulus zebrinus* was not collected in 1999, and common carp was not found in 1999 or 2001. Adults of bluehead sucker, flannelmouth sucker, channel catfish, and common carp were rarely collected in secondary channels in autumn; almost all individuals collected were less than 100 mm TL and were probably age 0. Red shiner, fathead minnow, speckled dace, plains killifish, and western mosquitofish specimens ranged in size from about 30 to 100 mm TL and likely represented all age-classes of these species.

Total nonnative fish density was greatest (10.131 fish/m^2) in 2000, the year of lowest spring and summer discharge, and lowest (0.249 fish/m^2) in 1999 (Table 3). The greatest density of red shiner, common carp, and western mosquitofish was in 2000, but fathead minnow density was greatest in 1995, channel catfish peaked in 1993, and the

TABLE 3.—Density (fish/m^2) of native fishes, nonnative fishes, and commonly collected species in San Juan River secondary channels, New Mexico and Utah, 1993–2001.

Species	1993	1994	1995	1996	1997	1998	1999	2000	2001
Natives	1.366	0.480	0.618	0.101	0.233	0.322	0.084	0.099	0.139
Speckled dace	1.032	0.394	0.561	0.076	0.208	0.314	0.077	0.066	0.128
Bluehead sucker	0.155	0.008	0.024	0.007	0.007	0.001	0.003	0.009	0.001
Flannelmouth sucker	0.179	0.078	0.032	0.018	0.014	0.007	0.003	0.023	0.009
Nonnatives	3.120	3.463	3.851	3.963	0.562	0.537	0.249	10.131	1.602
Red shiner	2.298	1.902	2.346	2.172	0.381	0.389	0.225	8.553	1.358
Common carp	0.003	0.003	0.005	0.001	0.007	0.001	0.000	0.164	0.00
Fathead minnow	0.662	0.894	1.375	1.316	0.065	0.085	0.016	0.766	0.154
Channel catfish	0.092	0.083	0.035	0.034	0.022	0.072	0.003	0.014	0.013
Western mosquitofish	0.043	0.262	0.077	0.428	0.006	0.059	0.002	0.622	0.060

greatest density of plains killifish was in 1994. Red shiner was the most common species in all years. Its density was often an order of magnitude greater than that of the next most common species. Fathead minnow was the second or third most-common species. Western mosquitofish was third-most common in 1996 and 2000, the years of lowest summer discharge.

Total native fish density was highest (1.366 fish/m^2) in 1993, the year of highest spring discharge, and was lowest (0.084 fish/m^2) in 1999, a year of low spring discharge but high summer discharge. The density of each commonly collected native species was also highest in 1993, but the year of lowest density varied among these species. Among all species, speckled dace was second- or third-most common species in all years, except 1996 and 2000 (the years of lowest summer discharge).

Based upon MANOVA, spring discharge had a significant effect on autumn native fishes density (Wilk's lambda [WL] = 0.317, $P < 0.0001$). There was no reach effect (WL = 0.772, $P = 0.523$) or interaction between reach and spring discharge (WL = 0.584, $P = 0.097$). Individual tests for speckled dace, bluehead sucker, and flannelmouth sucker each showed a significant (all P-values < 0.002) and positive association with spring discharge (Figure 2). Collectively, nonnative fishes autumn density was significantly affected (WL = 0.326, $P = 0.003$) by spring discharge and by reach (WL = 0.266, $P = 0.019$), but there was no interaction between these variables (WL = 0.376, $P = 0.117$). Individually, only western mosquitofish varied significantly by reach ($F = 3.95$, $P = 0.035$), and it was negatively associated with spring discharge ($F = 7.45$, $P = 0.013$). Summer discharge had no effect on native or nonnative fish density ($P > 0.100$). An overall association of number of days of summer discharge less than 14 m^3/s and native fishes was significant (WL = 0.232, $P = 0.013$), without a reach or interaction effect. Individual tests showed a significant negative effect only on speckled dace density ($F = 7.914$, $P = 0.009$). There also was a weak overall effect of the number of days summer discharge was less than 14 m^3/s on nonnatives (WL = 0.119, $P = 0.072$), but no reach or interaction effect. This pattern was driven by the positive response of red shiner, common carp, and western mosquitofish to periods of low flow ($F = 13.441$, $P < 0.001$; $F = 7.503$, $P = 0.015$; and $F = 11.593$, $P < 0.001$ for individual tests, respectively). However, individual tests for both common carp and western mosquitofish also revealed a significant interaction between reach and periods of low flow ($P < 0.03$), largely because this response was strongest in the upstream reaches where both species were most common.

Discussion

The premise that regulated flow regimes negatively affect native fish assemblages and its corollary that such flows enhance the survival of nonnative fishes has been proffered in several studies (e.g., Stanford and Ward 1986; Marchetti and Moyle 2001; Brouder 2001). Conversely, in some unregulated streams, native fish faunas remain comparatively intact and nonnative fishes are uncommon (Baltz and Moyle 1993). Various mechanisms have been suggested to explain observed differential responses of native and nonnative fishes to natural and altered flow regimes (Galat and Zweimüller 2001; Bunn and Arthington 2002). Several studies (e.g., Minckley and Meffe 1987; Brouder 2001; Marchetti and Moyle 2001; Valdez et al. 2001) suggested that elevated flows flushed or displaced nonnative fishes and that native fishes were "resistant" to displacement or rapidly repopulated stream reaches after displacement. Several of the aforementioned studies (e.g., Stanford and Ward 1986; Minckley and Meffe 1987) provided the framework and justification for the partial restoration of a natural flow regime as a management tool to restore imperiled species and to conserve the native fish fauna of the San Juan River. It was proposed that a more natural flow regime would restore or enhance those abiotic attributes that native fishes require and would be detrimental to nonnative fishes by diminishing their habitat or disrupting critical life stages.

Navajo Reservoir has been operated to mimic a natural flow regime since 1993. Reservoir releases to simulate spring runoff was the primary feature of the natural flow regime mimicked during the study. This reservoir management yielded annual spring runoff patterns after 1993 more similar to those prior to the closure of Navajo Dam in 1962 than those which occurred between 1962 and 1991. Our expectation that native fishes would respond positively (based on changes in their autumn densities) to increased spring discharge was confirmed, and the response of each common native species (speckled dace, flannelmouth sucker, and bluehead sucker) was significant. Although nonnative species were collectively negatively affected by high spring flows, western mosquitofish was the only species to show a strong response. Neither native nor nonnative fishes were negatively af-

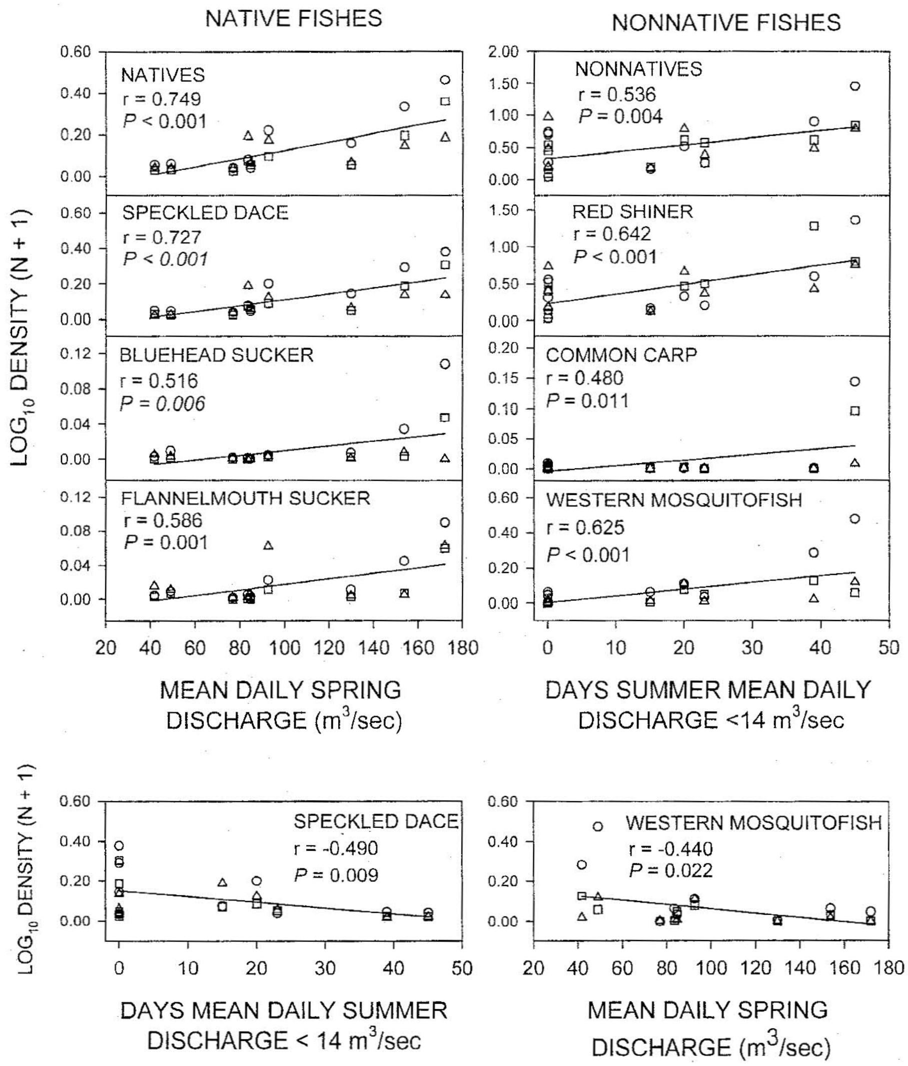

FIGURE 2.—Correlations between (1) autumn density of all native fishes and common native species with mean daily spring discharge; (2) autumn density of speckled dace and days of mean daily summer discharge less than 14 m^3/s; (3) autumn density of nonnative fishes and three common nonnative species and days of mean daily summer discharge less than 14 m^3/s; and (4) autumn density of western mosquitofish and mean daily spring discharge. The study area consisted of secondary channels in the San Juan River, New Mexico and Utah, from 1993 to 2001; circles = reach 5 densities, squares = reach 4 densities, and triangles = reach 3 densities (see Figure 1).

fected by elevated summer flows. Both native and nonnative fish densities, however, were influenced by the number days of summer discharge less than 14 m^3 in that speckled dace density declined and red shiner, common carp, and western mosquitofish densities generally increased during years with extended low discharge.

The positive response of native fishes to elevated spring discharge was at least partially related to the life history attributes and habitat affinities of each species. Each common native species spawns in cobbled riffles (D.L.P. and K.B.G., unpublished data), and speckled dace and bluehead sucker are both commonly associated with riffles throughout their lives (Rinne 1992; Gido and Propst 1999). Elevated spring flows clean cobble and gravel bars of fine sediments, thereby increasing spawning and macroinvertebrate habitat quality.

Elevated spring flows had no discernable effect on the autumn density of any nonnative species except western mosquitofish. This result appears to contradict previous conclusions of ours (Gido et al. 1997) and Marchetti and Moyle (2001) on the negative effects of elevated spring discharge on nonnative fish abundance. Minckley and Meffe (1987) found that elevated flows greatly diminished nonnative fishes in southwestern streams, but these findings were based on data from canyon-bound streams. In such environments, lateral movement of fishes onto the flood plain (where water velocities were typically lower than in the river channel) during high flows was not possible and fish were thus displaced. The San Juan River, in our study area, flowed through a broad, alluvial valley, and flooded lowlands provided refuge during spring runoff. Alternatively, lack of negative effects on common nonnative species (except western mosquitofish) simply may have been because spring flows were insufficient to displace them. The highest spring instantaneous discharge of 351 m^3/s between 1993 and 2001 was commonly exceeded prior to the closure of the Navajo Dam. In addition, spring runoff during our study usually was limited to May and June, whereas predam runoff extended from March through June. Thus, the duration and volume of spring runoff during our study (plus reduced amplitude) were insufficient to displace nonnative fishes. Alternatively, the perceived absence of a response may have been a consequence of when we sampled. Studies reporting a decrease in nonnative abundance based their results on sampling shortly after a recession of elevated flows. We sampled about 3 months after spring runoff recession, and the immediate effects of elevated spring discharge therefore were not detected. Another, and we believe more plausible, explanation involves consideration of life history traits of each common nonnative species, particularly red shiner (which regularly comprised ≥75% of the nonnative assemblage). Most, and likely all, reproduction of red shiner, fathead minnow, western mosquitofish, and plains killifish occurred during summer (July through September). Each of these small-bodied, short-lived species is capable of producing large numbers of young each year; the females of at least red shiner, fathead minnow, and western mosquitofish are capable of multiple clutches during a single season (Krumholz 1948; Gale and Buynak 1982; Gale 1986), and individuals of these species are able to spawn their first summer of life (Markus 1934; Krumholz 1948; Marsh-Matthews et al. 2002). Elevated spring discharge may have diminished the abundance of these nonnatives, but their (except for western mosquitofish) reproductive potential was sufficiently high to overcome or offset losses associated with elevated spring discharge. In addition, elevated spring flows likely enhanced red shiner (a crevice spawner; Gale 1986) reproductive success by cleansing riffles of fine sediments.

There was no relationship between summer mean daily discharge and native or nonnative fish densities (collective). Densities of red shiner, common carp, and western mosquitofish, however, were positively related to days with discharges of 14 m^3/s or less. The optimal spawning temperatures for red shiner and western mosquitofish are above 20–22°C (Gale 1986; Hubbs 2000), and a water temperature of 20°C was regularly exceeded in secondary channels when discharge was less than 14 m^3/s (D.L.P. and K.B.G., unpublished data). In addition to spawning during summer, the tolerance of these species to elevated water temperatures and depressed dissolved oxygen (Matthews and Hill 1979; Hubbs 2000) likely contributed to their high autumn densities following low summer flows.

The construction of dams and subsequent flow regulation have been identified as primary reasons for the decline of native fishes of the American Southwest and the establishment of noxious nonnative species (Richter et al. 1997). Consequently, restoration of natural flow regimes often is proposed as a management strategy to restore native fish faunas (e.g., Poff et al. 1997). However, in a system such as the San Juan River, with considerable institutional restraints (e.g., flood control and meeting intra- and interstate water delivery obligations), only partial restoration of a natural flow regime is possible. In our nine-year study we found that native fishes responded positively to reservoir releases designed to mimic natural spring runoff, but nonnative fish density was largely unaffected. Several summer-spawning nonnative fishes, however, responded positively to extended low summer flows. Thus, if natural flow regime mimicry included the provision of low summer flows (similar to those that occurred historically), summer-spawning nonnative fishes would benefit, perhaps to the detriment of native fishes. Conservation of the native fish fauna in the San Juan River and similar systems will be challenging because life history strategies and broad environmental tolerances of problem nonnative fishes enable them to overcome transitory deleterious flows. Until ways to eradicate or control nonnative fishes are devised, management efforts should focus on maximizing reproductive and recruitment success of native fishes through flow manipulations to enhance their habitats and to avoid flows that benefit nonnative fishes.

Acknowledgments

Field work was accomplished with the assistance of numerous colleagues, most notably L. A. Ahlm, T. Bingham, M. J. Buntjer, T. Chart, J. E. Davis, C. M. Hoagstrom, A. L. Hobbes, J. A. Jackson, and R. D. Larson. Our research has benefited from discussions with K. R. Bestgen, J. E. Brooks, W. J. Matthews, W. L. Minckley, F. K. Pfeifer, and S. P. Platania. The comments, suggestions, and insights of P. B Moyle and H. M. Tyus on earlier drafts of this manuscript were particularly helpful. S. Gottlieb prepared Figure 1. This study was supported by the U.S. Bureau of Reclamation and the New Mexico Department of Game and Fish under the auspices of the San Juan River Basin Recovery Implementation Program. Scientific collecting permits were provided by the Navajo Nation, States of Utah and New Mexico, and the U.S. Fish and Wildlife Service.

References

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications 3: 246–255.

Bliesner, R., and V. Lamarra. 2000. Hydrology, geomorphology, and habitat studies: San Juan River Basin Recovery Implementation Program. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

Brouder, M. J. 2001. Effects of flooding on recruitment of roundtail chub, *Gila robusta*, in a Southwestern river. Southwestern Naturalist 46:302–310.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 31:492–507.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland.

Galat, D. L., and I. Zweimüller. 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20:266–279.

Gale, W. F. 1986. Indeterminate fecundity and spawning behavior of captive red shiners—fractional, crevice spawners. Transactions of the American Fisheries Society 115:429–437.

Gale, W. F., and G. L. Buynak. 1982. Fecundity and spawning frequency of the fathead minnow—a fractional spawner. Transactions of the American Fisheries Society 111:35–40.

Gido, K. B., and D. L. Propst. 1999. Habitat use and association of native and nonnative fishes in the San Juan River, New Mexico and Utah. Copeia 1999: 321–332.

Gido, K. B., D. L. Propst, and M. C. Molles. 1997. Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah. Environmental Biology of Fishes 49:417–434.

Hubbs, C. 2000. Survival of *Gambusia affinis* in a hostile environment. Southwestern Naturalist 45:521–522.

Krumholz, L. A. 1948. Reproduction of the western mosquitofish, *Gambusia affinis* (Baird and Girard) and its use in mosquito control. Ecological Monographs 17:1–43.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11:530–539.

Markus, H. C. 1934. Life history of the blackhead minnow (*Pimephales promelas*). Copeia 1934:116–122.

Marsh-Matthews, E., W. J. Matthews, K. B. Gido, and R. L. Marsh. 2002. Reproduction by young-of-year red shiner (*Cyprinella lutrensis*) and its implications for invasion success. Southwestern Naturalist 47: 605–610.

Matthews, W. J., and L. G. Hill. 1979. Influences of physicochemical factors on habitat selection by red shiner, *Notropis lutrensis* (Pisces: Cyprinidae). Copeia 1979:70–81.

Meffe, G. K. 1985. Predation and species replacement in American southwestern fishes. Southwestern Naturalist 30:173–187.

Minckley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream fish communities of the arid American Southwest. Pages 96–104 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Rinne, J. N. 1992. Physical habitat utilization of fish in a Sonoran Desert stream, Arizona, southwestern United States. Ecology of Freshwater Fishes 1:35–41.

Ruppert, J. B., R. T. Muth, and T. P. Nesler. 1993. Predation on fish larvae by adult red shiner, Yampa and Green rivers, Colorado. Southwestern Naturalist 38: 397–399.

Stanford, J. A., and J. V. Ward. 1986. Fish of the Colorado River system. Pages 385–402 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers: Research and Management 12:391–413.

Tyus, H. M. 1992. An instream flow philosophy for recovering endangered Colorado River fishes. Rivers 3:27–36.

Tyus, H. M., B. D. Burdick, R. A. Valdez, C. M. Haynes, T. A. Lytle, and C. R. Berry. 1982. Fishes of the upper Colorado River basin; distribution, abundance, and status. Pages 12–70 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, editors. Fishes of the upper Colorado River system: present and future. American Fisheries Society, Bethesda, Maryland.

Tyus, H. M., and J. F. Saunders, III. 2000. Nonnative fish control and endangered fish recovery: lessons from the Colorado River. Fisheries 25(9):17–24.

Valdez, R. A., T. L. Hoffnagle, C. C. McIvor, T. Mckinney, and W. C. Liebfried. 2001. Effects of a test flow on fishes of the Colorado River in Grand Canyon, Arizona. Ecological Applications 11:686–700.